

INTRASPECIFIC AND INTERSPECIFIC COMMUNICATION
ON PRAIRIE DOG COLONIES
BLACK TAILED PRAIRIE DOGS AND BURROWING OWLS

by

Rebecca Dyckes Bryan

B.A., University of Colorado Denver, 1997

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Rebecca D. Bryan

has been approved for the

Department of Integrative Biology

by

Michael Wunder, Advisor

Michael Greene

Laurel Hartley

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Bryan, Rebecca D. (M.S., Biology)

Interspecific and intraspecific communication on prairie dog colonies: black-tailed prairie dogs and burrowing owls.

Thesis directed by Assistant Professor Michael Wunder.

This thesis is a compilation of research from two different yet related projects. The common thread in these projects is alarm calling and communication on black-tailed prairie dog (*Cynomys ludovicianus*) colonies. I considered both intra-specific communication: how black-tailed prairie dogs communicate with each other, and inter-specific communication: how another species, the Western Burrowing Owl (*Athene cunicularia*), benefits from prairie dog communication. The first chapter consists of background information pertinent to communication and alarm calling, and introduces both study species. The second and third chapters are formatted as stand-alone manuscripts reporting the results of my field studies. I have also included appendices of additional data analysis information that, while important, for various reasons was not included in the prepared manuscripts.

The form and content of this abstract are approved. I recommend its publication.

Approved: Michael Wunder

DEDICATION

I dedicate this work to my husband and best friend, George.

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It is impossible to acknowledge every single person who contributed to the completion of this project, but I do want to name a few very important individuals without whom I would never have gotten this far. First and foremost I want to say thanks to my parents, Martha and Doug, who have always known what I am capable of achieving even when I can't see it. And to the best big sister ever, Melissa: thanks for giving me much needed teaching and learning advice. Huge thanks to George for playing the role of supportive husband in every way; I could never have done this without you. Also, I want to thank my committee members: Mike Greene, for reinforcing my love of animal behavior (it's so cool!); Laurel Hartley, for encouraging me, offering ideas and advice, and most importantly, friendship; and last, but certainly not least, Mike Wunder, for introducing me to this project idea and letting me run with it – even when I sometimes ran into dead ends. As much as I struggled with it at the time, I will always appreciate that you gave me the freedom to find those dead ends for myself, and that you were there to help me find my way back out.

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CHAPTER

I. INTRODUCTION

This project examines both interspecific and intraspecific communication that takes place on black-tailed prairie dog (*Cynomys ludovicianus*) colonies. Black tailed prairie dogs emit alarm calls in the presence of threats, and these alarms are specific to the type or immediacy of the perceived threat (Smith et al. 1977, Hoogland 1995). Relatives and distant kin are alerted to danger and are therefore more likely to be able to avoid it. This enhances the fitness of the alarm caller, since its offspring and relatives are more likely to avoid the threat (Hoogland 1995). I hypothesize that these alarm calls serve an unintended purpose as well, alerting another species living on the colony to threats. Western Burrowing owls (*Athene cunicularia*) have high nesting success on black-tailed prairie dog colonies. Although there are multiple hypotheses about why this is the case, (Desmond et al. 2000, Beradelli et al. 2010) one unexplored idea is that burrowing owls attend and respond to the alarm calls black-tailed prairie dogs emit. This would enhance the birds' survival on colonies and offer a further explanation of increased nesting success.

Prairie Dogs

Black-tailed prairie dogs (hereafter, prairie dogs) are the most common of the 5 prairie dog species found in North America, which include Gunnison's prairie dogs (*Cynomys gunnisoni*), white-tailed prairie dogs (*Cynomys leucurus*), Mexican prairie dogs (*Cynomys mexicanus*), and Utah prairie dogs (*Cynomys parvidens*). The black-tailed prairie dog is an herbivorous rodent of the sciurid family. Adult weights average about 1

kg, and full grown black-tailed prairie dogs stand 30-35 cm high. They are native to the western Great Plains of North America, and their range extends from southern Canada through Montana, the Dakotas, Wyoming, Colorado, Utah, Arizona, and Texas (Figure I.1).

Prairie dogs are diurnal fossorial mammals that live in colonies. Average colony area is 20 to 60 hectares, and colonies can contain from 25 to upwards of one million individuals (Bishop and Culbertson 1976). Prairie dogs live in territorial family groups known as coterie within the colonies. Coterie normally consist of one male, 2 to 4 breeding females, and juvenile offspring (Hoogland 1995). Unlike other rodent species, prairie dogs breed only once a year. Females give birth to litters of 1 to 7 pups in the spring between the months of March and June, and care of pups is shared among the female coterie members (Hoogland 1995). Young emerge from the burrows for the first time in mid- to late- May. Predators of adult and juvenile prairie dogs include American badgers (*Taxidea taxus*), swift foxes (*Vulpes velox*), coyotes (*Canis latrans*), black-footed ferrets (*Mustela nigripes*), golden eagles (*Aquila chrysaetos*), and red-tailed hawks (*Buteo jamaicensis*). Bullsnares (*Pituophis catenifer*) and prairie rattlesnakes (*Crotalus viridis*) will predate newborn and juvenile prairie dogs (Halpin 1983).

The geographic range of the black-tailed prairie dog has decreased dramatically over the past 200 years. Fossil records indicate that prairie dogs had a relatively stable, large range from 40,000 years ago until the early 19th century (Lomolino and Smith 2001, Forrest 2005). Since then their geographic range has shrunk considerably: the historic occupied habitat of the black-tailed prairie dog is estimated at 35 to 40 million hectares, but is currently estimated to be less than 1 million hectares (USFWS 2011). This is a

direct result of habitat conversion for agriculture, human land development and consequent eradication efforts (Miller et al. 1994), and the introduction of plague (*Yersinia pestis*) (Lomolino and Smith 2001, Antolin 2002). The decline of active black tailed prairie dog colonies has not only affected this species, but several others as well, including small mammals and birds such as mountain plover (*Charadrius montanus*) and burrowing owl (*Athene cunicularia*) (Miller et al. 1994, Wuerthner 1997, McDonald et al. 2004, Knopf 2008, Shipley et al. 2008, Cully et al. 2010).

Prairie dogs can be considered a keystone species (sensu Power 1996): their influence on plant and animal communities is disproportionately large compared to their relative abundance (Kotliar et al. 1999, Kotliar 2000, but see Stapp 1998). Prairie dogs also serve the function of ecosystem engineers (sensu Jones et al. 1994) because they modify their environment in ways that influence resource availability to other organisms. Prairie dog colonies have lower vegetation height, lower standing biomass, and more bare ground than the surrounding grassland (Whicker and Dettling 1988). Prairie dog colonies provide a large prey base for carnivores and offer shelter and nesting habitat for various species of birds and small mammals (Barko 1997, Wuerthner 1997, Cully et al. 2010). In short- and mixed-grass prairies of North America, prairie dog towns are associated with higher bird species richness and abundance than un-colonized areas (Agnew et al. 1986, Barko et al. 1999). Prairie dog grazing on colony sites supplies better visibility of insect prey for insectivorous bird species (Barko 1997, Schneider et al. 2006), better access to seed for granivorous birds (Agnew et al. 1986), better detection of predators for ground-nesting birds (Knopf 2006), and the prairie dogs themselves serve as a food source for raptors (Barko et al. 1999).

Burrowing Owls

Western Burrowing Owls (*Athene cunicularia*) are small ground-dwelling raptors. Burrowing owl nesting habitat consists primarily of open treeless areas on plains and prairies with short vegetation (McDonald et al. 2004). They often nest in prairie dog burrows in active prairie dog colonies on the Great Plains. The burrowing owl breeding range extends to the middle of Alberta and Saskatchewan in the north, and their winter range extends south to Honduras. They can be found in Florida and Mexico year-round (Figure I.2). A burrowing owl home range is around 2.5km² (Poulin et al. 2011).

Burrowing owls begin nesting as early as March, but in northern latitudes nesting may not begin until May. Only female burrowing owls incubate the eggs; males of the mated pair hunt and forage for both adults and young hatchlings. Burrowing owl young are altricial and completely dependent on parental care until they are 2 months old (Poulin et al. 2011). Juvenile survival is around 57%, and mortality rates for these birds are highest when they first leave the nest - before they can fly - and when they first become independent from adult owls (Davies and Restani 2006).

Burrowing owl predators include badgers, long-tailed weasels (*Mustela frenata*), skunks (*Conepatus spp.*, *Spilogale spp.*), coyotes, and domestic dogs (*Canis familiaris*) and cats (*Felis domesticus*). Other raptors (hawks, owls, and falcons) also hunt burrowing owls. Burrowing owl eggs and chicks can be predated by prairie rattlesnakes and bullsnakes. During the nesting season, burrowing owls will dive or fly at mammalian predators near the nest. To avoid avian predators, burrowing owls will escape into their burrows (Poulin et al. 2011). Young burrowing owls will respond to a nest disturbance with a rattlesnake-like buzzing vocalization which is thought to deter predators (Owings

et al. 2002). If a nest is predated, burrowing owls will disperse and re-nest in a different burrow, as long as it is early enough in the breeding season (Catlin and Rosenberg 2008). Burrowing owls will return to the same nesting site year after year if they are successful there (McDonald et al. 2004). Within the nesting site, owls may make use of more than one burrow; nearby burrows can act as escape holes or alternate nest sites if the original site becomes unusable (Winchell 1994), and young disperse to the nearby burrows after their first 2 to 3 weeks of life (Poulin et al. 2011).

Burrowing owls show a preference for prairie dog burrows on active colonies. A study on National Grasslands on the Great Plains showed owls present on 69% of active prairie dog colonies, but they were present on only 11% of inactive colonies (Sidle et al. 2001). Burrowing owls are crepuscular, nocturnal, or diurnal depending on the time of year. During breeding season, they are most active at dawn and dusk, but are alert and active during the day as well (Poulin et al. 2011).

In Colorado, burrowing owls are found more commonly on than off prairie dog colonies (Smith and Lomolino 2004, Plumpton and Lutz 1993). Burrowing owls have shown an overall declining trend in population in recent years (Desmond et al. 2000), and the Colorado Division of Wildlife (2011) lists burrowing owls as a state threatened species. Because of their close association on with prairie dogs, the decline in prairie dog geographic range may have large effect on how well owls survive. Conservation efforts for burrowing owls are closely tied with those for the black-tailed prairie dog.

Alarm Calling and Eavesdropping

In many species living in social groups, individuals rely on collective vigilance to increase their foraging time while simultaneously decreasing their risk of predation. One or a few group members monitor their surroundings for potential threats while others forage (Bell et al., 2009). Scanning the surroundings is synchronized between group members (Pays et al. 2007) such that each group member has an opportunity to forage without having to maintain strict individualized vigilance. Vigilant animals emit alarms when they detect a risk. Alarm signals can be visual, auditory, or chemical depending on the species. For species using audible alarm calls, the alarm signals vary in specificity; some calls are urgency-based only, and others encode information about the particular type of threat (review: Macedonia and Evans 1993; Furrer and Manser 2009). A collective-vigilance and alarm-calling system minimizes the energy required by any single individual to avoid predators (Beuchamp and Ruxton 2007).

Prairie dogs are one such species that uses a sophisticated auditory alarm system to warn other colony members of potential danger. In the presence of perceived danger, prairie dogs emit an anti-predator bark (Hoogland 1995). This anti-predator bark varies in rate and in acoustic structure depending on the predator threat and, possibly, the mode of approach (Hoogland 1995, Fredrickson and Slobodchikoff 2007). Barks vary in frequency, duration, and harshness depending on the situation (Smith et al. 1977). Single barks are uncommon, while continuous bouts of chirping can go on for several minutes at a time. Black-tailed prairie dogs also display a “jump-yip” behavior which can occur in territorial disputes and chases, in response to low risk stimuli, or in the absence of any apparent stimulus at all (Smith et al. 1976). Senkiw (2007) hypothesized that the jump-

yip may also serve to provide information about vigilance among group members, alerting foraging prairie dogs in the vicinity to the caller's vigilance status.

Hollen and Radford (2009) define three important aspects of animal alarm calling behavior as follows: 1) call production, where a call having a specific acoustic structure is created, 2) call usage, the context in which the call is used, and 3) call responses, the reactions of others to the call. Normally all three of these aspects apply within a single species. For example, if a prairie dog (1) produces an alarm call (2) in the presence of an aerial predator, (3) other prairie dogs will react with the appropriate avoidance behavior, whether they have themselves seen the predator or not (Kiriakis and Slobodchikoff 2006). However, there are cases where aspects (1) and (2) will lead to a response in a different species. This is known as heterospecific eavesdropping.

Heterospecific eavesdropping has been studied extensively in several bird species (Magrath et al. 2007, 2009), and evidence of eavesdropping on another species' alarm calls has been noted in non-avian species as well. Evidence of social and non-social animals eavesdropping on avian alarm calls has been documented in several species of mammals and some reptiles (Table I.1). Banded mongooses (*Mungos mungo*) increase their vigilance in response to plover (*Vanellus spp.*) alarms (Mueller and Manser 2008), and red squirrels (*Sciurus vulgaris*), increase vigilance and escape responses when they eavesdrop on alarm calls given by Eurasian jays (*Garraulus glandarius*) (Randler 2005). Schmidt et al. (2008) demonstrated that eastern chipmunks (*Tamias striatus*) eavesdrop on tufted titmouse (*Baeolophus bicolor*) alarms, and show a stronger anti-predator response to that indirect cue than they show to a direct predator cue. Rasa (1983) showed that dwarf mongooses (*Helogale undulata rufula*) forage with two species of hornbill

(*Tockus deckeni* and *T. flavirostris*), and benefit from eavesdropping on those birds' alarm calls. This relationship is so important that the mongooses often will not begin to forage without hornbills present, since their presence significantly enhances mongoose survival (Rasa 1983). Foraging activity decreases and vigilance increases in Gunther's dik-dik antelope (*Madoqua guentheri*) when they hear go-away bird (*Corythioides leucogaster*) alarm calls (Lea et al. 2008). Two species of iguanas, the Galapagos marine iguana (*Amblyrhynchus cristatus*) and the Madagascan spiny tailed iguana (*Oplurus cuvieri cuvieri*) eavesdrop on closely associated birds: Galapagos mocking birds (*Nisomimus parvulus*) and paradise flycatchers (*Terpsiphone mutata*), respectively. Galapagos marine iguanas respond to mocking bird alarm calls (but not song) with increased vigilance behavior (Vitousek et al. 2007), and spiny tailed iguanas will also increase their vigilance in response to flycatcher alarms, but not their songs (Ito and Mori 2010).

In most documented eavesdropping cases a bird species eavesdrops on another bird species, a mammal species eavesdrops on another mammal species, or a mammal species eavesdrops on a bird species. In an exception to this, Rainey et al. (2004) found evidence of a bird species that eavesdrops on a mammalian alarm call. Yellow casqued hornbills (*Ceratogymna elata*) eavesdrop on alarm calls that Diana monkeys (*Cercopithecus diana*) produce. The hornbills do not respond to every alarm vocalization Diana monkeys make, however. Diana monkeys have different alarm calls in response to different predators, and the hornbills are able to differentiate between those alarms, adding to the usefulness of the eavesdropping behavior. Hornbills only use energy to respond to alarm calls for predators that they share with the monkeys, and do not waste

energy responding to alarms for other, unshared predators (Rainey et al. 2004). In all eavesdropping cases, the eavesdropping individuals are able to enhance their own fitness by paying attention to other species' alarms and taking anti-predator measures, usually in the form of increased vigilance.

If burrowing owls living on prairie dog colonies take advantage of a similar eavesdropping behavior, it might add to the explanation of their increased nesting success on prairie dog colonies. Not only do they benefit from ready-made burrows, shortened grass, higher prey availability, and a possible predator dilution effect provided by the prairie dogs (Plumpton and Lutz 1993, Desmond et al. 2000, Orth and Kennedy 2001), they also have a built-in look-out system alerting them to possible threats. Eavesdropping on prairie dog alarm calls could be very valuable to burrowing owls.

Figures and Tables

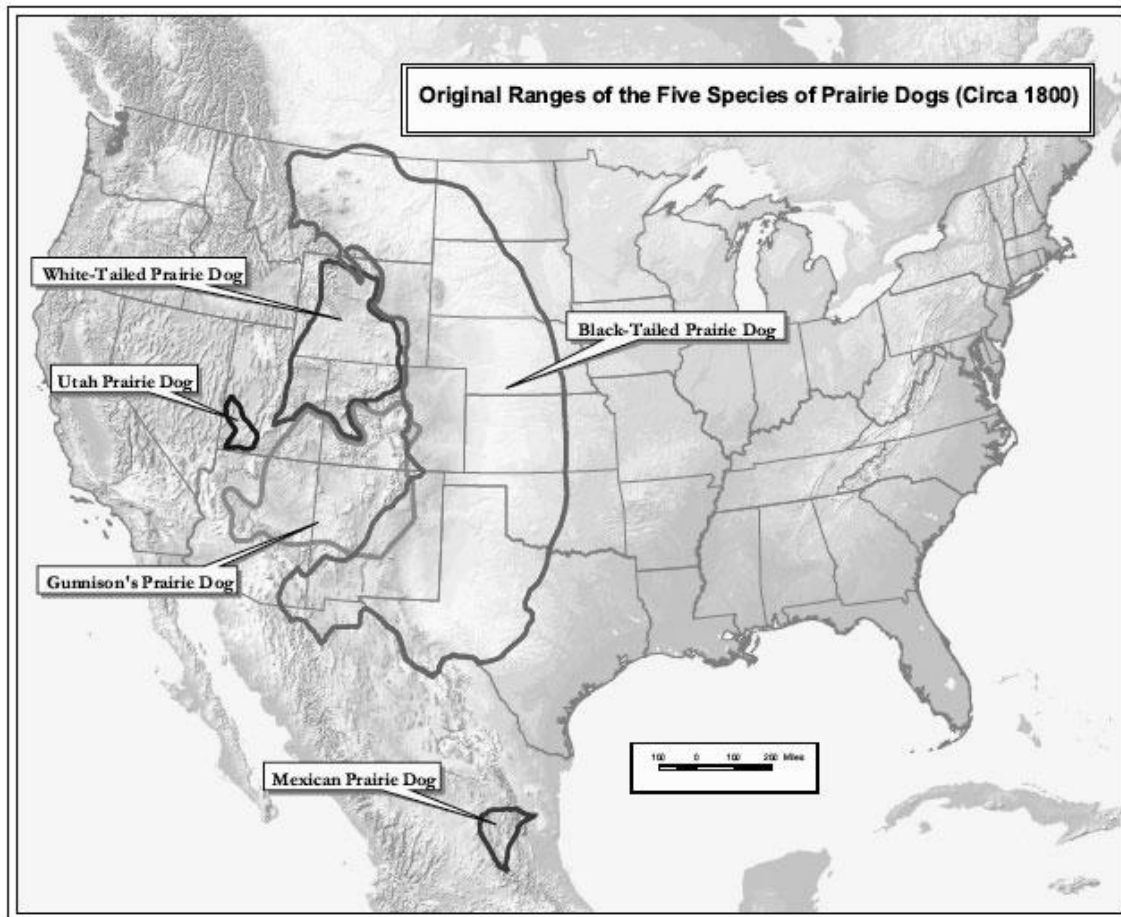


Figure I.1 Historic Range of Prairie Dogs.

Range of the five prairie dog species in the United States. Black tailed prairie dogs (*Cynomys ludovicianus*) have the broadest range, stretching from Canada to Northern Mexico. Map downloaded from:

http://www.defenders.org/images/programs_policy/Imperiled_Species/prairie_dog/pd_historic_range.jpg

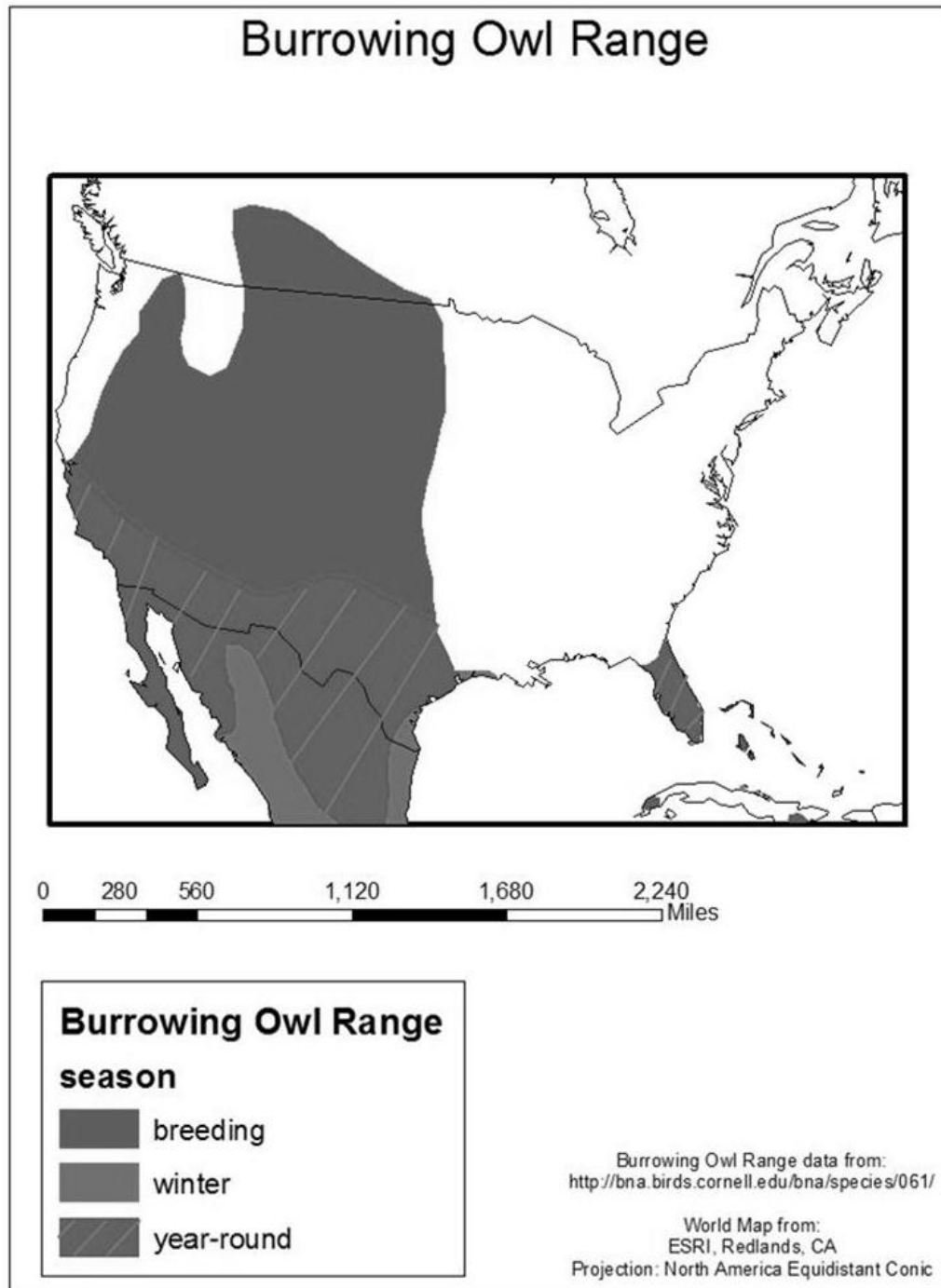


Figure I.2 Historic Range of Burrowing Owls.

Breeding and wintering ranges of the Western Burrowing Owl (*Athene cunicularia*) in the United States.

Table I.1 Cross-taxa heterospecific eavesdropping examples.

A selection of cross-taxa eavesdroppers that use avian alarm calls to their advantage.

Avian alarm caller	Responding heterospecific	Eavesdropper's response	Reference
Hornbills (<i>Tockus deckeni</i> and <i>T. flavirostris</i>)	Dwarf mongoose (<i>Helogale undulata rufula</i>)	Decreases own vigilance behavior in presence of hornbills and attends to hornbill alarms while foraging	Rasa 1983
Eurasian jay (<i>Garraulus glandarius</i>)	Red squirrel (<i>Sciurus vulgaris</i>)	Increases vigilance and escape responses when jays alarm	Randler 2005
Galapagos mocking bird (<i>Nisomimus parvulus</i>)	Galapagos marine iguana (<i>Amblyrhynchus cristatus</i>)	Increases vigilance in response to alarms, but not in response to song	Vitousek et al. 2007
White-bellied go-away bird (<i>Corythioides leucogaster</i>)	Gunther's dik-dik antelope (<i>Madoqua guentheri</i>)	Decreases foraging activity, increases vigilance in response to alarm calls	Lea et al. 2008
Plovers (<i>Vanellus spp.</i>)	Banded mongoose (<i>Mungos mungo</i>)	Increases vigilance in response to alarm, but does not appear to respond differently when alarm urgency varies	Mueller and Manser 2008
Tufted titmouse (<i>Baeolophus bicolor</i>)	Eastern chipmunk (<i>Tamias striatus</i>)	Stronger anti-predator response to the indirect cue than to direct predator cues	Schmidt et al. 2008
Paradise flycatcher (<i>Terpsiphone mutata</i>)	Madagascan spiny tailed iguana (<i>Oplurus cuvieri cuvieri</i>)	Increases vigilance in response to alarm calls	Ito and Mori 2010

CHAPTER

II. CHARACTERISTICS OF BLACK-TAILED PRAIRIE DOG (*Cynomys ludovicianus*) ALARM CALLS IN RESPONSE TO SIMULATED PREDATOR THREATS

Abstract

I presented potentially threatening stimuli to a colony of black-tailed prairie dogs (*Cynomys ludovicianus*) in Boulder County, Colorado and recorded the subsequent vocalized alarm calls. I measured characteristics of prairie dog vocalizations in response to three stimuli: a model snake, a domestic dog, and a human on foot. For each trial, I analyzed the following characteristics of the spectrogram of the first distinct bark in response to the stimulus: 1) the duration of the bark (time in seconds), 2) the central frequency, 3) low frequency, and 4) high frequency (Hz) of the vocalization, 5) the first and third quartile frequencies (Hz), and 6) the average power (db) of the vocalization. I compared these structural characteristics of the alarm calls across stimulus type and found that there were significant differences in bark duration, IQR bandwidth, and frequency change between the human stimulus and the model snake stimulus. The greater duration and higher frequency of the snake alarm bark may indicate that prairie dogs perceived the simulated snake as a more imminent, localized, and urgent threat and that the human may or may not have been perceived as a threat. I was unable to draw conclusions about more specific semantic encoding contained in the alarm from these measurements.

Background

In many species living in social groups, individuals rely on collective vigilance to increase their foraging time while simultaneously decreasing their risk of predation. One or a few group members monitor their surroundings for potential threats while others forage (Bell *et al.*, 2009). Scanning the surroundings is synchronized between group members (Pays *et al.*, 2007) such that each group member has an opportunity to forage without having to maintain strict individualized vigilance. Vigilant animals may emit audible alarm calls when they detect a threat. Auditory alarm signals vary in specificity; some calls are urgency-based only, and others encode information about the particular type of threat (review: Macedonia and Evans, 1993; Furrer and Manser, 2009). Alarm-calling systems like these minimize the energy required by any single individual to avoid predators (Beuchamp and Ruxton, 2007). Several studies of alarm calling social animals have shown that if an animal produces a specific alarm call in the presence of a given predator or a given threat level, other group members will react with the appropriate avoidance behavior whether they have themselves seen the predator or not (Seyfarth and Cheney, 1984, 2003; Kiriazis and Slobodchikoff, 2006; Furrer and Manser, 2009).

Gunnison's prairie dogs (*Cynomys gunnisoni*) use alarm calls with referential specificity. The calls differ in structure based on predator and mode of approach (Ackers and Slobdchikoff, 1999). For instance, the alarm call for a hawk is structurally distinct from the alarm call for a coyote, and prairie dogs take different evasive measures based on these call differences. There is also evidence that Gunnison's prairie dogs can recognize individuals of the same predator species and alarm based on that individual's threat level (Ackers and Slobodchikoff, 1999).

Another species of prairie dog, the black-tailed prairie dog (*Cynomys ludovicianus*) also uses a sophisticated alarm system to warn other colony members of potential danger. In the presence of perceived danger, black-tailed prairie dogs emit an anti-predator alarm bark (Hoogland, 1995): repeated chirps about 0.1s duration. The anti-predator bark may vary in rate and in sound structure depending on the predator threat and, possibly, the mode of approach (Smith *et al.*, 1977; Hoogland, 1995; Fredrickson and Slobodchikoff, 2007). Black-tailed prairie dogs also display a “jump-yip” behavior which can occur in territorial disputes and chases, in response to low risk stimuli, or in the absence of any apparent stimulus at all (Smith *et al.*, 1976). Halpin (1983) and Loughry (1987) noted that jump-yips occurred most commonly in the presence of snakes, and Owens and Loughry (1985) posit that the jump-yip is a reaction to a less immediate threat while an alarm bark indicates more urgency.

Fredrickson and Slobodchikoff (2007) showed that black-tailed prairie dogs might also encode information about predator threat in their alarm calls. Alarm calls were significantly different in structure when a human previously seen with a weapon, indicating a potential high predatory threat, approached and when a human associated with food, indicating a low predatory threat, approached.

Based on the studies of Gunnison’s prairie dog vocabulary and observations of black-tailed prairie dog vocalization behaviors, I tested the hypothesis that presenting black-tailed prairie dogs with different potentially threatening stimuli would elicit alarm calls that were measurably different in structure. I used a domestic dog (*Canis lupus familiaris*), a simulated snake, and a human as stimuli.

Materials and Methods

Study Area Experimental trials took place on Carolyn Holmberg Preserve at Rock Creek Farm in southeast Boulder County, Colorado (Figure II.1). This public open space property covers approximately 1100 acres, and is a popular recreation area for hikers, runners, anglers, and bicyclists. The property is surrounded by a shopping mall, major highway, railroad, and neighborhood subdivision. The area was primarily native short-grass prairie before its conversion to rangeland, and there are some parcels of uncultivated land containing primarily native vegetation, such as buffalo grass (*Buchloe dactyloides*), blue grama (*Bouteloua gracilis*), and prickly pear cactus (*Opuntia polyacantha*). All trials conducted took place on rangeland which included, along with native grasses, non-native grasses and forbs such as cheatgrass (*Bromus tectorum*) and field bindweed (*Convolvulus arvensis*). All of the trial locations were within one half mile of wetlands in the preserve. Common plant species in the wetland areas are plains cottonwood (*Populus sargentii*) and coyote willow (*Salix exigua*). The habitat is also home to prairie dog predators including coyotes (*Canis latrans*), red-tailed hawks (*Buteo jamaicensis*), bull snakes (*Pituophis catenifer*), and western rattlesnakes (*Crotalus viridis*). Grazing cattle were rotated around the study site. I did not make recordings on colonies when cattle were present.

Field Methods I presented stimuli to prairie dogs daily between 0500 h and 1100 h from 25 May to 29 July 2010. I digitally recorded all audible responses to each stimulus presented. Stimuli included 1) a domestic dog (German shepherd mix) walking into the colony, 2) a rubber snake pulled through the colony on fishing line, and 3) a human walking into the colony at 3-4 kph, toward a single focal prairie dog. I also presented prairie dogs with a helium-filled Mylar[®] balloon to simulate an airborne threat (Appendix

I). However, the presentation of the balloon added confounding variables, particularly noise, that likely affected response behaviors, so analysis of those trials has been omitted from results.

To ensure that the prairie dogs were not associating me with the presented stimuli, I remained hidden in a blind throughout all trials, with the exception of the human trial. Individual animals were not marked, but I rotated the placement of blinds over nine different areas of the colony to decrease the probability of recording responses from the same individuals repeatedly. Each of the nine testing sites was at least 100m from any of the others, and I estimate that at least 20 different animals contributed to my samples. At each testing location, I gave prairie dogs in the area two to three days to acclimatize to the presence of the blind prior to running any trials. I only ran domestic dog trials on days that I arrived before prairie dogs had begun their morning foraging. I kept the dog on a 15-foot lead anchored behind the blind during all presentations. The dog was very accustomed to prairie dogs, and did not vocalize or attempt to chase the prairie dogs at any time. For snake trials, I hid the snake at least 20 meters away from the blind under debris on-colony so that it would not be visible until I began the trial and started pulling it from behind the blind. To simulate a more natural smell, I also wrapped the snake in sheds from a bull snake. I alternated the presentation of two different observers (RDB and a technician) as the human stimulus. Because there were no systematic differences in the alarm calls in response to the two different people, I considered response alarm calls to both humans as one group.

In all trials, I waited until one or more prairie dogs were visible in the trial area before beginning. I made mp3 audio recordings using a Marantz®PMD661 digital

recorder (Mahwah, NJ) and AudioTechnica® shotgun microphone (Stow, OH), which was set up to protrude just outside of the blind, aimed at the prairie dog colony. I started recording 5 seconds before presenting a stimulus, and stopped recording when the stimulus was no longer visible to the prairie dogs or when they stopped reacting. I recorded calls from prairie dogs that were 15-60 meters from the blind. The microphone did not clearly pick up prairie dog vocalizations from farther than 60 meters away. Trial recordings lasted a minimum of one minute. At the end of each day, I downloaded the recordings into a computer running RavenPro 1.4® sound analysis software (Ithaca, NY).

Data Analysis For each alarm call recorded, I determined alarm rate by calculating the number of barks in a randomly selected 10 second interval during the stimulus presentation. I compared the averages of alarm rate across trials. For consistency in measuring acoustical structure, I used the first audible bark in response to each presented stimulus for analysis. I measured the duration of the bark (time in seconds), the central, low, and high frequencies (Hz) of the vocalization, the first and third quartile frequencies (Hz), the IQR bandwidth (difference between the first and third quartile frequencies) (Hz), and the average power of the vocalization (db; Figure II.2). From these measurements, I also calculated the change in frequency: the difference between the highest frequency and lowest frequency harmonic in the vocalization.

I used R® version 2.11.1 (©2010: The R foundation for statistical computing) to run one-way ANOVA tests on each of the above measurements by stimulus. I used post-hoc multiple comparisons analysis using Tukey's HSD to determine significant differences between measurements by stimulus.

Results

I was able to take measurements from a total of 33 snake trials, 34 human trials, and 15 dog trials. If sonograms were unclear or had more than one prairie dog bark overlapping, I discarded them from my measurements. Because I could only run dog trials on days that I arrived before the prairie dogs emerged, I was unable to run as many dog trials. Other stimuli allowed me to run trials at different blinds on the same day, so I did not have this constraint.

Prairie dogs alarmed in response to each of the presented stimuli. Responses immediately followed the appearance of each stimulus. There were no significant differences among trials in the average number of barks per random 10 second interval; prairie dogs alarmed at an average rate of 16.2 ± 5.6 barks/ten seconds, with dog predator responses showing the highest amount of variance.

Duration One-way ANOVA showed a significant effect of stimulus type on the length of the first bark in response to the stimuli ($F_{2, 79} = 7.0$, $P = 0.0014$). Specifically, post-hoc multiple comparisons showed that the response to the snake stimulus was longer in duration than that for the human stimulus ($P = 0.013$), but the average response durations for snake and human stimuli were not significantly different from that recorded for the dog stimulus (Table II.1).

Frequency Central, low, and high frequency measurements alone did not show significant differences based on stimulus type presented. However, there was a significant effect of stimulus type on the average change in frequency for each alarm call ($F_{2, 79} = 3.3$, $P = 0.039$). Post-hoc multiple comparisons showed that snake alarms were associated with a higher average change in frequency than human alarms ($P = 0.04$), but neither differed significantly from average changes for dog alarms (Table II.1).

IQR bandwidth The effect of stimulus type on average IQR bandwidth was also significant ($F_{2, 79} = 4.4$, $P = 0.015$). Post-hoc multiple comparisons showed that alarms in response to the snake stimulus had a smaller IQR bandwidth than those in response to the human stimulus ($P = 0.029$). Dog alarm barks were not significantly different from either stimulus (Table II.1).

Average Power There was a significant effect of stimulus type on the average power of alarm barks ($F_{2, 79} = 7.2$, $P = 0.013$). Specifically, post-hoc multiple comparisons of average power showed that calls in response to the snake stimulus were higher power than those in response to the human stimulus ($P = 0.0012$). Responses did not differ significantly between human and dog or snake and dog (Table II.1).

Discussion

My results support the hypothesis that black-tailed prairie dog alarm calls differ in acoustical structure based on the stimulus presented. These results support previous research on Gunnison's prairie dogs (Slobodchikoff *et al.*, 1991; Ackers and Slobodchikoff, 1999) and black-tailed prairie dogs (Smith *et al.*, 1977; Halpin, 1983; Owens and Loughry, 1985; Fredrickson and Slobodchikoff, 2007) suggesting that alarm calls vary in structure according to predator threat.

Alarm calls in response to the snake stimulus showed a higher maximum power (db) than alarm calls in response to the human stimulus. Because I do not know exact distances to the prairie dogs recorded in each trial, it is unclear if the calls were higher in power simply due to the distance to the alarming prairie dog or if the increased decibel level was reflective of the stimulus. I could not control for distance of prairie dogs that responded, but because my recordings were at random distances across all samples, it

seems unlikely that any distance-based bias influenced the results. In fact, the consistently random nature of the sampling distance offers further support to the statistically different results being a result of differences in stimulus rather than in distance.

Change in frequency indicates the difference between the highest frequency and lowest frequency harmonic in the vocalization, and IQR bandwidth indicates the difference between first and third quartile frequencies (Figure II.2). Both of these measurements were significantly different in the snake response than the human response: the difference between the lowest and highest harmonic was larger in the snake than in the human, but the difference in the third and first quartile frequencies was smaller. This combination of factors would result in a different sound timbre.

In the presence of the snake stimulus, I recorded two distinct types of vocalization: a normal alarm bark and a jump-yip vocalization (Figure II.3). Based on previous observations, the latter was likely a snake-specific alarm call. The sonogram's shape and the behavior accompanying the vocalization are both similar in structure to those described by Smith et al. (1976), Owings and Owings (1979), and Loughry (1987). However, I observed this call on only 3 of 30 snake presentations. For data analysis, I used the alarm bark that coincided with the snake presentation and not the jump-yip.

The acoustical differences I measured may convey information about the immediacy of the threat. Longer vocalizations at a higher calling rate may indicate more urgent contexts (review: Taylor and Reby, 2010). Alarming prairie dogs in the vicinity of the model snake emitted significantly longer barks in response to the snake stimulus than to the human, but the rate of calling did not vary significantly. It is possible that the threat

of the snake was more immediate than that of the approaching human, resulting in a more potentially dangerous situation and a longer vocalization. The preserve where trials took place is a very heavily used recreation area in an outdoors-oriented community. Prairie dogs encounter humans and dogs in this area on a daily, and at times an hourly basis. Snakes are common, but are likely considered more of a threat in this area than are dogs or humans.

The snake-specific jump-yip call occurred on three occasions during trials. The spectrogram associated with this call had a triangular shape distinctly different from the parallel lines on the spectrograms associated with more general alarm barks in response to the model snake (Figure II.3). A sound that rises and falls equally in a chevron shape may indicate ambivalence on the part of the vocalizing animal (Morton, 1977): the animal has conflicting motivations as to whether it should stay or flee, resulting in the animal doing a combination of both of those behaviors. This is manifested in rapid movements and conspicuous displays known as mobbing (Lord *et al.*, 2009). Mobbing is a common anti-predator behavior seen in many birds and mammals in response to a predator or an unknown stimulus. An individual giving a mobbing call and/or displaying a mobbing behavioral pattern signals others in the area to join. Whether or not others join, the behavior pattern reflects the ambivalence noted above. The chevron shape of the snake-specific jump-yip which accompanied both tentative stalking and aggressive attacks on the model snake supports this hypothesis, although stalking and mobbing of the snake occurred without the jump-yip as well; on 18 such occasions, prairie dogs directly approached the snake stimulus. On four of these occasions they attacked and tore pieces off of the model snake. Prairie dogs retreated from the model snake only twice,

and one of those times the retreating animal was a juvenile. I did not observe more than one adult prairie dog approaching and attacking the model snake at any given time, but did observe other adult prairie dogs in the vicinity observing the model and the attacking prairie dog from nearby.

The observation of more alarm behaviors than jump-yip behaviors in response to the snake stimulus contrasts with results from previous studies where the jump-yip response to snakes was more commonly recorded (Halpin, 1983; Loughry, 1987). Perhaps this has to do with the sudden appearance of the snake in the colony when pulled out of its hiding place. Macedonia and Evans (1993) noted that some alarm-calling mammals use different alarm calls to differentiate high threat from lower threat predators, but will use a high-threat predator call if danger from a normally low-threat predator is immediate. If a jump-yip indicates a lower-threat predator, but that lower-threat predator appears quite suddenly and/or unexpectedly, a more urgent alarm may be used instead. It is also possible that the snake model was not recognized as a snake, and the prairie dogs were alarming in response to a novel threat.

Ackers and Slobodchikoff (1999) showed that Gunnison's prairie dogs are able to encode referential specificity in their alarm calls. Through discriminate function analysis, they showed that alarm calls for a model skunk, a model coyote, and an oval control showed qualitative and quantitative differences, and were consistent for an individual prairie dog. This suggests that random variation in sonogram characteristics among prairie dogs is less relevant than systematic variation in sonogram characteristics resulting from encoded semantic information. Using a similar analysis method, Fredrickson and Slobodchikoff (2007) showed that black-tailed prairie dogs might also

encode semantic information about predator type in their alarm calls. Because I did not mark individuals, I could not be sure that I presented different stimuli to the same animal at a trial site, and so I did not use discriminate function analysis to incorporate all measured parameters in statistical analysis. However, I was still able to quantify differences in alarm calls based on the stimulus type. It is therefore quite likely that the prairie dogs recorded in this study are also encoding qualitative information about potential threats in their alarm calls.

Because black-tailed prairie dog alarm calls serve to alert relatives and distant kin of danger (Hoogland, 1995), the more specific the call is to a threat, the more likely it is that those relatives and distant kin will react appropriately. Results of this study suggest that black-tailed prairie dog alarm calls contain information about threat urgency. However, although urgency information may be contained in the call, the existence of the information does not necessarily make it informative to other prairie dogs (Seyfarth and Cheney, 2003), and I did not specifically observe prairie dog responses to these calls. The mobbing behavior witnessed in response to the snake model indicates a possibility that the alarm calls convey information to other prairie dogs in the area, but without more specific playback experiments, I do not know if these behaviors were a result of visual or auditory cues.

Figures and Tables

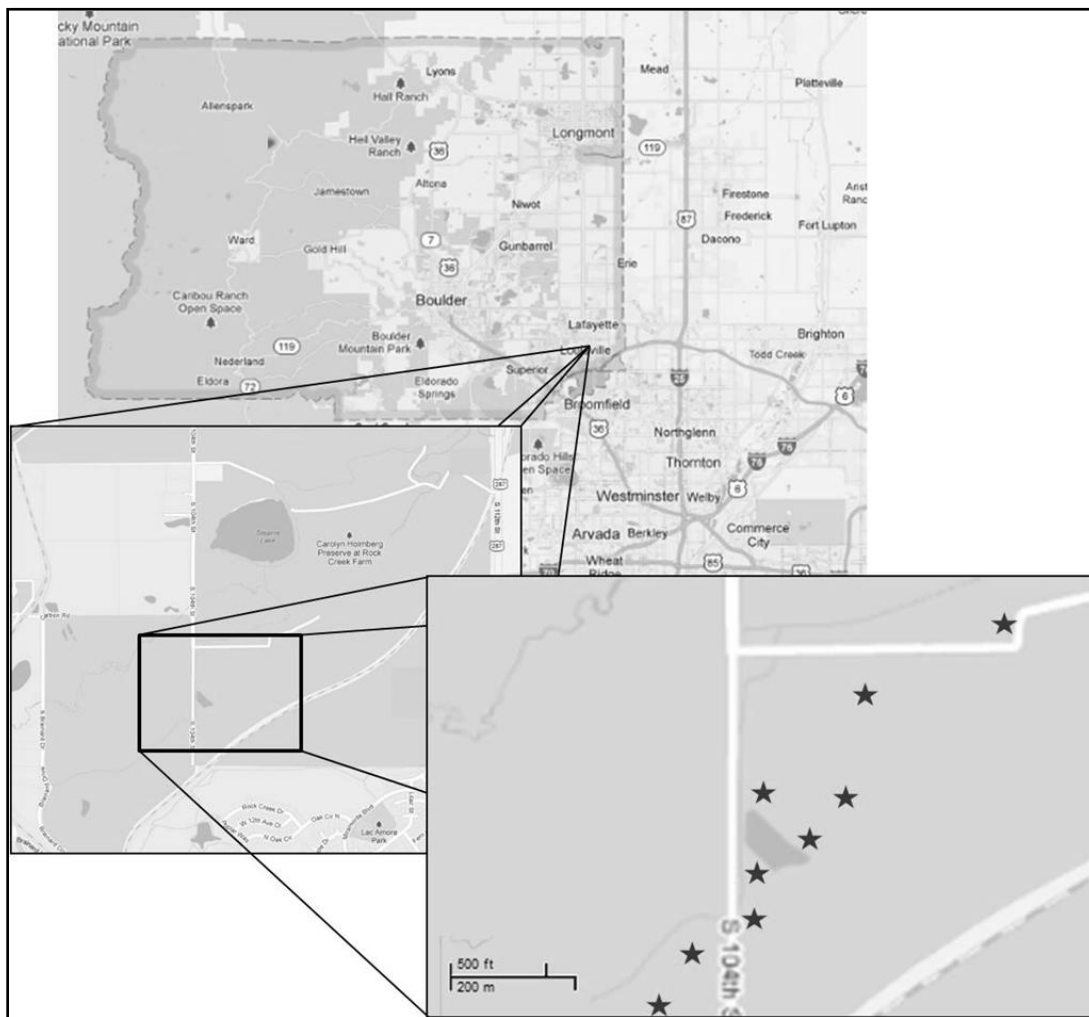


Figure II.1 Map of Prairie Dog Study Area, Boulder County, CO.

All prairie dog response trials took place at the Carolyn Holmberg Preserve at Rock Creek Park, an Open Space property in Boulder County, Colorado. Inset: blind locations marked with stars. Blinds and trials were rotated around these nine sites over the two month period.

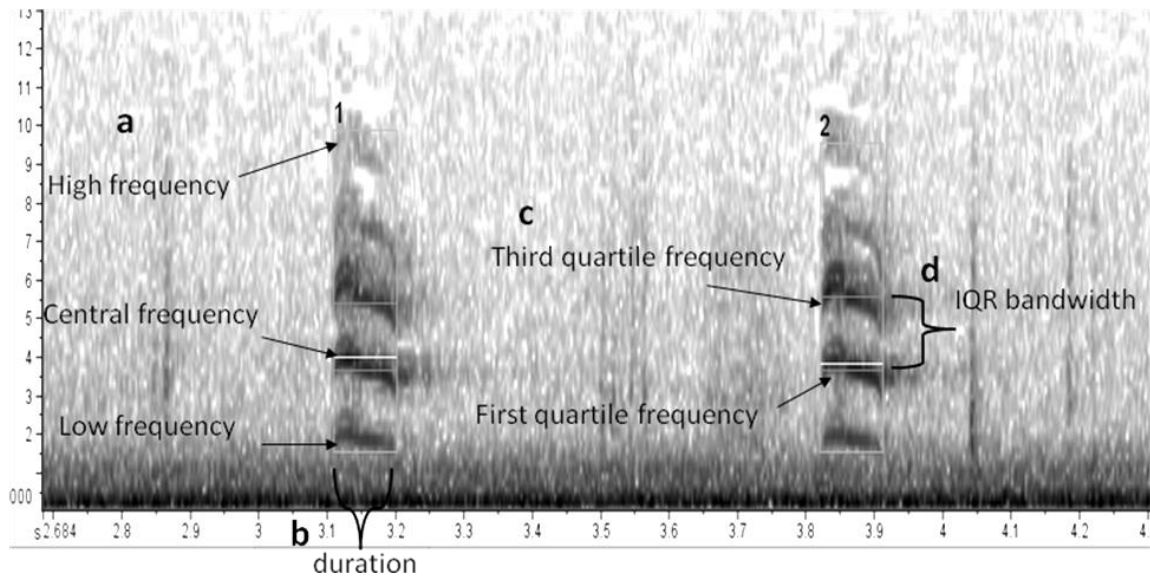


Figure II.2 Spectrogram measurements.

Spectrogram of two alarm barks in response to the domestic dog. Measurements of (a) central, low, and high frequencies (in Hertz), (b) duration (Δ time), (c) the first and third quartile frequencies, and (d) IQR bandwidth. Measurements were made using RavenPro®1.4 software.

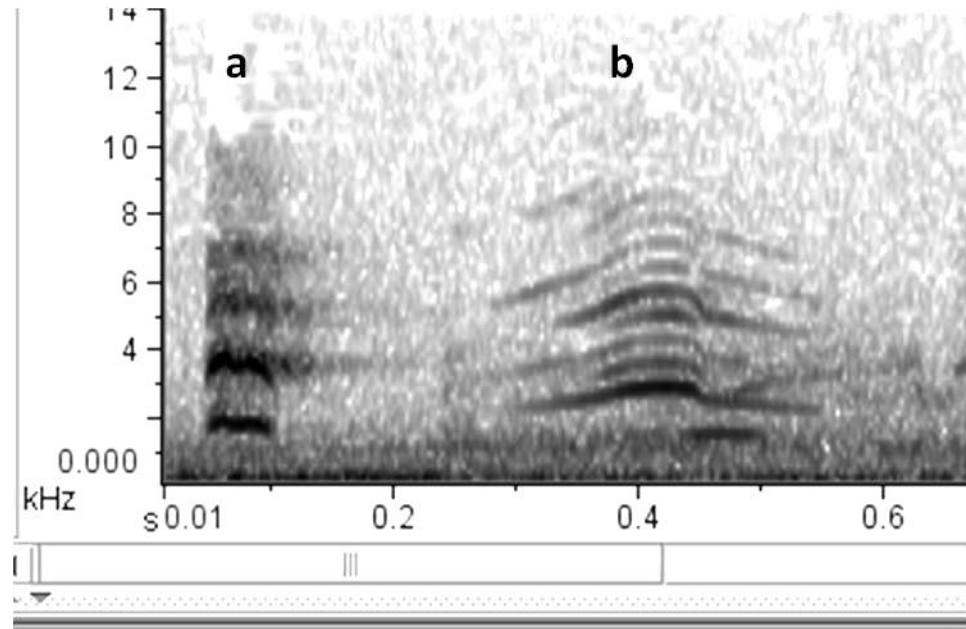


Figure II.3 Spectrogram of Snake Responses.

Spectrogram of (a) normal bark in response to the snake stimulus, (b) jump-yip recorded in presence of snake stimulus. The normal bark is much shorter in duration, with less harmonic variation, and the jump-yip vocalization has a distinctive chevron shape seen in animal vocalizations that are commonly associated with mobbing behaviors.

Table II.1 Structural attributes of alarm spectrograms.

Mean \pm standard error for the first alarm bark in response to a predator stimulus. Stimuli that share the same superscript letters are not significantly different ($P > 0.05$). Different superscript letters indicate significant differences in the means ($P < 0.05$).

	mean Δ time (ms)			mean Δ frequency (Hz)		
dog ($n = 15$)	0.074	\pm	0.0035 ^{ab}	6314.1	\pm	221.58 ^{ab}
snake ($n = 33$)	0.076	\pm	0.0029 ^a	7126.5	\pm	188.81 ^b
human ($n = 34$)	0.063	\pm	0.0022 ^b	6267.1	\pm	302.83 ^a
	mean IQR bandwidth (Hz)			mean average power (db)		
dog ($n = 15$)	1986.8	\pm	282.24 ^{ab}	64.93	\pm	2.47 ^{ab}
snake ($n = 33$)	1247.6	\pm	178.99 ^a	59.03	\pm	1.14 ^b
human ($n = 34$)	1889.9	\pm	162.71 ^b	66.66	\pm	1.67 ^a

CHAPTER

III. BURROWING OWLS EAVESDROP ON ALARM CALLS OF BLACK TAILED PRAIRIE DOGS

Abstract

I investigated whether Western Burrowing Owls (*Athene cunicularia*) nesting on black-tailed prairie dog (*Cynomys ludovicianus*) colonies responded to playbacks of prairie dog alarm calls. Western burrowing owls are closely associated with black-tailed prairie dogs in Colorado and neighboring states on the Great Plains of the United States. Owls have high nesting success on prairie dog colonies: they have pre-made nest-sites and good foraging habitat, and prairie dogs may act as an alternate prey source for predators. Owls nesting on prairie dog colonies may eavesdrop on the prairie dogs as well: owls attending and responding to the alarm calls that the prairie dogs emit may enhance their survival and nesting success on colonies. I performed playback experiments with three different treatments: a prairie dog alarm call, a biological control (cattle mooing), and a non-biological control (an airplane engine). Owls reacted more quickly to the prairie dog alarm than to the biological control. They increased their vigilance behaviors significantly in response to playbacks of the alarm, but did not show an increased reaction to either the biological or the non-biological control. My results suggest that owls nesting on prairie dog colonies eavesdrop on, and increase their vigilance in response to, prairie dog alarm calls.

Key words: Burrowing Owl (*Athene cunicularia*), eavesdropping, black-tailed prairie dog (*Cynomys ludovicianus*), alarm calling, vigilance

Introduction

When an individual animal gathers information about the environment it might produce a cue (a vocal or chemical signal) in response to that information for the benefit of other group members or kin. When the cue is produced, there is the potential for unintentional recipients as well (Goodale et al. 2010). Animals sharing a common habitat and common predators will sometimes take advantage of each others' vigilance by eavesdropping on their neighbors, particularly when the information comes in the form of a vocal alarm call. Heterospecific eavesdropping, when members of a different species acquire and benefit from the cue another species produces, has been studied extensively in birds. Magrath et al. (2007) and Fallow et al. (2011) found that different bird species with similar predators are able to cue in to each others' alarm calls when they hear them. Mobbing behaviors in many bird species are a result of responses to heterospecific alarms (Chu 2001, Johnson et al. 2003, Nocera and Ratcliffe 2010).

Evidence of social and non-social animals eavesdropping on avian alarm calls has been documented in mammalian and reptilian species as well. Mammalian examples include red squirrels (*Sciurus vulgaris*), dik-dik antelope (*Madoqua guentheri*), banded mongooses (*Mungos mungo*), and Eastern chipmunks (*Tamias striatus*) (Randler 2005, Lea et al. 2008, Mueller and Manser 2008, Schmidt 2008), and reptilian examples include Galapagos marine iguanas (*Amblyrhynchus cristatus*) and Madagascan spiny tailed iguanas (*Oplurus cuvieri cuvieri*) (Vitousek et al. 2007, Ito and Mori 2010). Rainey et al. (2004) found evidence of a more unusual eavesdropper: a bird which eavesdrops on a non-avian alarm call. Yellow casqued hornbills (*Ceratogymna elata*) eavesdrop on alarm calls of Diana monkeys (*Cercopithecus diana*). In this particular case of eavesdropping,

the birds differentiate between alarm calls they hear: they only respond to alarm calls for predators that they share with the monkeys, and not to alarm calls for other, unshared predators (Rainey et al. 2004). In all cases, eavesdropping individuals are able to enhance their own fitness by paying attention to other species' alarms and taking anti-predator measures, usually in the form of increased vigilance.

Western burrowing owls (*Athene cunicularia*) are listed as a species of special concern in several states in the Great Plains, including Montana, Oklahoma, Utah, and Wyoming (Poulin et al. 2011), and are listed as a state-threatened species in Colorado (Colorado Division of Wildlife 2011). Western burrowing owls (hereafter, burrowing owls or owls) are closely associated with black-tailed prairie dogs (*Cynomys ludovicianus*) in these areas, and the decline in black-tailed prairie dogs (hereafter, prairie dogs) due to management and sylvatic plague has been correlated with declines in burrowing owl populations (Desmond et al. 2000). Burrowing owls have high nesting success on prairie dog colonies, and are found more often on than off prairie dog colonies in the Western Great Plains (Holroyd et al. 2001). Burrowing owls commonly nest on prairie dog colonies with high burrow densities (Plumpton and Lutz 1993), and show a preference for active prairie dog colonies over abandoned colonies (Restani et al. 2001, Sidle et al. 2001). Multiple hypotheses have been put forth to explain this association between owls and prairie dog colonies. The disturbances prairie dogs create provide pre-made nest sites, and the short grass provides good foraging habitat (Poulin et al. 2011). Also, having prairie dogs nearby may cause a dilution effect if prairie dogs act as an alternative prey source for predators (Desmond et al. 2000). Desmond et al. (2000) and Beradelli et al. (2010) suggested that burrowing owls nesting on black-tailed prairie dog

colonies may eavesdrop on the prairie dogs as well: owls could attend and respond to the alarm calls that the prairie dogs emit. This would enhance the birds' survival on colonies and offer a further explanation of increased nesting success.

Burrowing owls use vocal alarm signals to alert each other to dangers, and those alerted (young or a nearby member of a pair) take appropriate actions to avoid the danger (Coulombe 1971). Burrowing owls sharing a habitat with another species that uses an alarm calling behavior (eg. prairie dogs or ground squirrels) may increase their vigilance when they hear an alarm from that species. Black-tailed prairie dogs emit alarm calls in the presence of predatory threats to alert relatives and distant kin of danger (Hoogland 1995). Burrowing owls, especially eggs and chicks, share predators with prairie dogs: American badgers (*Taxidea taxus*), coyotes (*Canis latrans*), red-tailed hawks (*Buteo jamaicensis*), and possibly prairie rattlesnakes (*Crotalus viridis*) and bullsnakes (*Pituophis catenifer*) predate both prairie dog and burrowing owl young (Halpin 1983, Coulombe 1971). Burrowing owl adults that eavesdrop on alarming prairie dogs can potentially learn when predators are approaching. If they increase their vigilance so they can respond appropriately to protect their young, they may enhance their fitness. In this study I tested whether burrowing owls respond to alarm calls that prairie dogs emit.

Methods

With permission from the Central Plains Experimental Range (CPER) and the National Forest Service, I conducted playback experiments on nesting owls on 14 different prairie dog colonies on the CPER and the Pawnee National Grasslands (PNG), located in Weld County, Colorado (Figure III.1). Experiments took place June through July, 2011. The Pawnee National Grasslands is a short-grass steppe ecosystem. The

average summer temperature is 22° C, and annual precipitation patterns can vary greatly. The average precipitation is 32cm, most commonly occurring between April and September. Precipitation manifests primarily as soaking rains in spring and as heavy localized thunderstorms in summer (SGS-LTER 2007). All experiments took place on prairie dog colonies on active ranchland, where vegetation included buffalo grass (*Buchloe dactyloides*), blue grama (*Bouteloua gracilis*), prickly pear cactus (*Opuntia Polyacantha*), scarlet globemallow (*Sphaeralcea coccinea*), saltbush (*Atriplex canescens*), and field bindweed (*Convolvulus arvensis*).

I conducted audio playbacks to owls nesting at 20 different locations on 14 active prairie dog colonies; several colonies had more than one nesting owl pair present, and when that was the case, I rotated trials between the active nests. I played 5 minute recordings of a randomized sequence of sounds to each bird: a prairie dog alarm call (the experimental treatment), a small airplane engine (a non-biological control treatment), cattle mooing (a biological control treatment), and ambient noise: intermittent birdsong, insect chatter, and other typical prairie sounds. I collected digital recordings of all sounds using a Marantz®PMD661 digital recorder (Mahwah, NJ) and AudioTechnica® shotgun microphone (Stow, OH). With the exception of the plane sound, which was collected near the Rocky Mountain Metropolitan Airport in Broomfield, Colorado, I recorded all sound stimuli on the PNG or the CPER. I recorded a herd of mooing cattle on open range on the PNG. I recorded prairie dog alarm call responses to a simulated snake predator (a toy snake pulled through the colony on a fishing line) on the CPER. I edited and combined the sounds using RavenPro 1.4® sound analysis software (Ithaca, NY). To ensure that the order the birds heard the sounds did not affect their responses, I created

three different treatment orders: Order 1 – prairie dog alarm (A), cattle mooing (biological control - B), airplane (non-biological control - N); Order 2 – B, N, A; and Order 3 – N, A, B. I started every trial with two min of ambient noise, and played stimulus sounds at a consistent volume and for the same amount of time across each trial. Each stimulus sound lasted 30 seconds, and the stimulus sounds were separated from each other by 1 min of ambient noise. I video recorded all trials using a JVC® Everio HD camcorder (Wayne, NJ). The time frame over which I ran trials coincided with the owls' nesting and chick-rearing stages. I did not know if this would affect adult vigilance patterns, so I divided all trials into two categories: "early" (when eggs have not yet hatched or have hatched but chicks have not yet surfaced) and "late" (when nestlings have surfaced and are beginning to disperse to nearby burrows). I then tested for differences in the adults' reactions to the stimulus cues based on nest stage.

Field Methods For each trial, I placed a SME-AFS portable field speaker (Elmont, NY) within 10 m of an active nest burrow. Owls usually flushed or ducked into the nest or a nearby burrow upon my arrival. Before beginning any playbacks, I waited in a blind for the bird to return to the vicinity of the speaker. For most trials the owl was within 10 to 20 m of the speaker. If the owl was more than 30 m away from the speaker, I did not score the trial in data analysis. The blind was 25 to 50 m from the nest burrow and/or focal owl for all trials. I used a pop-up hunting blind when it was not possible to use the truck as a blind. The truck was preferable because the owls are accustomed to seeing ranchers' vehicles on the prairie, so I used it as much as possible. I tested for differences in responses based on blind type when running analyses. Birds were unmarked, so it was not always possible to determine which experiments were repeated

on the same bird on different days. I rotated nest sites visited daily to ensure that I did not subject the same owl to the same tests consecutively.

Data Analysis I scored video files using JWatcher®1.0 software (Blumstein and Daniel 2007) using the ethogram in Table III.1. If the owl moved beyond 30 m of the speaker during the playback, or ducked underground and did not re-emerge, I included only those parts of the trial with the bird within 30 m of the speaker in the analysis. If there were prairie dogs vocalizing in the background of the video, I did not include the video in analyses.

For analysis, I classified responses as either “alert” or “relaxed.” Alert responses included vigilance (head turns), bobbing, locomotion, vocalizing, or stretching tall or squatting low while looking. Relaxed responses included preening, yawning, or sleeping (Table III.1). For the purposes of this study, I categorized foraging or looking down at the ground as relaxed behaviors, because the owls’ vigilance was directed toward prey and not toward external threats like predators. I calculated 1) latency to first alert response to presented sound cues (how quickly the owl reacted to the sound cue), and 2) the intensity of the response (how actively the owl responded) as determined by the number of alert responses within 10 sec of the presented cue. I considered each alert response mutually exclusive. I used R® version 2.11.1 (©2010: The R foundation for statistical computing) for all statistical analyses.

Analysis I – Latency to Response. I measured how quickly the owls responded to each sound stimulus, and compared these measurements by sound cue. To find the owls’ response times in milliseconds, I subtracted the start time of a given sound cue from the start time of the first alert response after that sound began playing. Because

results were not normally distributed, my data did not meet assumptions for parametric statistical tests. I used a Kruskal-Wallis rank-sum test to determine whether there were differences in median time to response in each of the sound stimulus categories: alarm, biological control, and non-biological control. In order to determine which categories showed significant differences from one another, I ran pair-wise Wilcoxon tests with Bonferroni adjustment.

Analysis II – Intensity of Response. Here I examined the rate of response to sound cues: i.e. how many alert responses the owl showed per unit time after hearing the sound cue. I categorized the owls' responses to the sound cues using behaviors within the first 10 sec during the playback of any given sound cue. I counted the number of alert responses during that 10 sec time frame and assigned the responses to one of three categories. Category 1 was defined as a “low” response rate: 0-2 alert behavioral responses; Category 2 was a “moderate” response rate: 3-4 alert behavioral responses; and Category 3 was a “high” response rate: 5 or more alert behavioral responses.

I administered a chi-squared analysis on these data with a Fisher's exact test given that one of the categories (Non-biological control, category 3) had less than 5 data points. Due to differences in response based on blind type (Fisher's Exact test $P < 0.01$), I analyzed truck and pop-up blind data separately.

Results

I conducted a total of 93 playback experiment trials on adult owls over the two-month period (truck blind $n = 51$, pop-up blind $n = 42$). I collected useful data from 58 of those trials (truck blind $n = 38$, pop-up blind $n = 20$), which included 16 different nesting pairs on 14 prairie dog colonies (Appendix II). Thirty-five of the 93 trials were censored

for various reasons, including excessive background noise: high winds; interruptions such as vehicles, prairie dogs, or cattle; owls leaving the experimental trial area; or too much distance between the video camera and the bird for accurate behavioral scoring.

Latency to Response Times There were no systematic differences between the owls' responses by sound presentation order by nest stage (2-way ANOVA stimulus and phenology: $F_{2, 151} = 0.62$, $P = 0.54$), or by blind (2-way ANOVA stimulus and blind: $F_{2, 151} = 0.32$, $P = 0.72$), so I pooled all data in subsequent analyses. Owls showed shorter median response times to the prairie dog alarm cue and the non-biological control cue as compared to the biological control sound (Pairwise Wilcoxon test with Bonferroni adjustment: Alarm and Non-biological cue $P=0.045$, Alarm and Biological control cue $P=0.028$). There was no significant difference in the median response time to the non-biological control sound cue and the prairie dog alarm sound cue ($P = 1.0$) (Table III.2, Figure III.2).

Intensity of Response There were no significant differences in response rate category (1 = low, 2 = moderate, 3 = high) based on the order the stimuli were presented (Fisher's Exact test: Alarm order: $P = 0.31$, Biological Control order: $P = 0.20$, Non-biological control order: $P = 0.32$) or nesting stage (Fisher's Exact test $P = 0.30$). When I conducted Chi-squared analysis by blind-type, I found fewer category 3 responses ($n=3$) than expected with the pop-up blind (Fisher's Exact test $P < 0.01$). Because of this discrepancy, I analyzed truck data and pop-up blind data separately.

In trials run from the truck ($n = 38$), owls showed more category 3 responses and fewer category 1 responses than expected when presented with the prairie dog alarm cue. When presented with the biological control sound cue, they showed fewer category 3

responses and more category 1 responses than expected. Owls showed expected responses to the non-biological sound cue (Fisher's Exact test $P = 0.024$; Figure III.3). In trials run from the pop-up ($n = 20$), there were no significant differences in observed and expected values for all sound cues (Fisher's Exact test $P = 0.15$). However, I recorded only three category 3 responses in trials run from the pop-up blind, and all of those were in response to the prairie dog alarm cue. This low number of responses makes statistical analysis difficult.

Discussion

Animals can indirectly receive information about their environment by observing information exchanges between other animals. The eavesdropping animal can obtain this information from visual, auditory, or chemical cues given by the donor. Eavesdroppers get information about traits such as size or strength of the donor, or they can gain information about resources and predation threats (Sih et al. 2009). For these reasons, eavesdropping can be useful in mate finding and competition, and is especially valuable in predator evasion.

Animals that use an anti-predator alarm calling system are an important indirect information source for eavesdropping individuals in their environments. When animals emit alarm calls, the calls may be urgency based (Furrer and Manser 2009), they may have predator specific information encoded (Seyfarth and Cheney 2003), and/or they may induce group members to mob a potential threat (Morton 1977). Animals that share a habitat, have similar predators, and are similar in body size to the alarm caller are likely to pay attention to those alarms because doing so can increase their fitness (Templeton and Greene 2007). Some eavesdroppers are able to accurately interpret the information

the alarms encode (Seyfarth and Cheney 1984,2003; Rainey 2004; Hetrick and Sieving 2012), and some eavesdroppers show more anti-predator behaviors in response to a heterospecific alarm call than they do to direct evidence of a predator (Schmidt et al. 2008). Eavesdropping behavior is common between species of birds and between species of mammals, and cross-taxa eavesdropping is effective in many systems as well.

My study shows an example of a cross-taxa eavesdropping network that likely enhances the fitness of the eavesdropper by alerting them to potential threats in their environments. I found that burrowing owls living on prairie dog colonies increased their vigilance behaviors in response to prairie dog alarm calls: the owls reacted more quickly to the prairie dog alarm sound cue than to a non-alarm biological sound cue (cattle mooing), and continued to show increased vigilance behaviors after their initial response.

Upon hearing the prairie dog alarm call, the owls had fewer category 1 (low rate) responses than expected based on chance alone; they showed significantly more category 2 (moderate rate) or category 3 (high rate) response rates than expected. However, the owls did not flee in response to the alarms and very rarely ($n = 2$) vocalized in the 10 seconds following the prairie dog alarm call. This potentially indicates that the owls were increasing their vigilance, but needed first-hand information before they would act on those cues.

Although the owls reacted equally quickly to the non-biological sound cue, they did not continue to show increased vigilance. The non-biological sound cue was a sudden loud airplane engine noise that did not particularly resemble any sounds that the owls were accustomed to hearing at the study site, with the possible exception of occasional passing trucks. It appears that this sudden noise startled the owls into a quick alert

response, but since the noise came from a single direction and was not accompanied by any physical apparition, it was likely not seen as an immediate threat. The owls did not flee nor increase their vigilance over the following 10 second interval.

The owls nesting on this study site are very accustomed to cattle, encountering them on a nearly daily basis. This might explain the birds' response (or lack thereof) to the biological control sound cue. Cattle moo to communicate with each other, and although some cow vocalizations may be in response to threats (Watts and Stookey 2000), cattle do not share predators with burrowing owls, and the presence of cattle on burrowing owl and prairie dog habitat is relatively recent from an evolutionary perspective. Owls and prairie dogs have shared habitat for thousands of years, whereas organized cattle ranching on the Great Plains did not begin until the late 1860s (ERS 2000), so even if eavesdropping made sense in this case, it might not have had time to evolve. Also, it may not be necessary for owls to become or to remain highly vigilant in the presence of cattle: it is possible that with the cattle nearby there is a reduced risk to the owls of predation as well as reduced foraging capabilities, both of which could result in lower vigilance over all.

Owls in this area have a very close association with prairie dogs; the owls live in abandoned burrows on active colonies and occasionally interact with foraging or cover-seeking prairie dogs that have gotten close to their nests by flying at them or vocalizing toward them (personal observation). Foraging black-tailed prairie dogs are generally quiet and intermittently vigilant. Black-tailed prairie dogs do not rely on a single sentinel keeping watch for the entire group; instead all individuals regularly survey their surroundings, and when a threat is detected, the individual detecting the threat will alert

others in the group with a bark alarm (Hoogland 1995). Like prairie dogs in the alarming animal's vicinity, owls in the area also increase their vigilance behaviors in response to the alarm in an attempt to ascertain the threat.

My data suggest that owls nesting on prairie dog colonies likely gain some benefit from eavesdropping on prairie dog alarm calls. Owls increasing their vigilance in response to a prairie dog alarm may be more aware of threats in their environment as a result. However, whether the owls are reacting to the urgency of the alarm or semantic information contained in the alarm is still unknown and deserves further exploration. In many eavesdropping species, eavesdroppers show some ability to differentiate alarm calls from non-alarm vocalizations (Vitousek et al. 2007, Goodale et al. 2010, Ito and Mori 2010), as well as predator-specific alarm calls from each other (Rainey 2004).

Eavesdroppers able to differentiate would have the advantage of saving energy required for increased vigilance by not responding to calls that do not indicate a threat to the eavesdropper. Rainey (2004) demonstrated that yellow casqued hornbills are able to distinguish between predator-specific calls given by Diana monkeys, and only show increased anti-predator behaviors when they hear the alarm for a shared predator. Like Diana monkeys, prairie dogs also emit predator-specific calls which differ in response to predator type and mode of approach (Fredrickson and Slobodchikoff 2007). Burrowing owls may possess the ability to differentiate between types of alarm calls. In this study we only looked at reactions to the snake predator alarm. Further studies of owl reactions to specific alarm and non-alarm calls could show whether owls are able to decipher the information coded in prairie dog alarms.

Figures and Tables

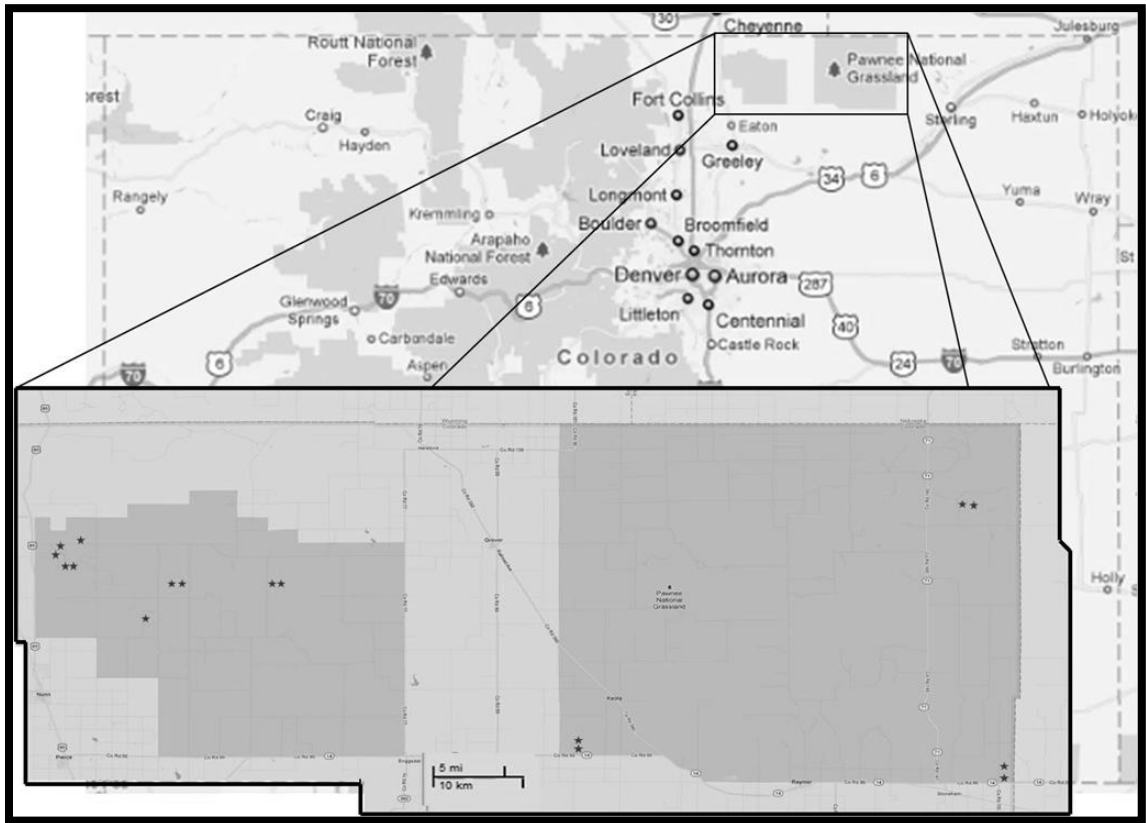


Figure III.1 Map of Burrowing Owl Study Area, Pawnee National Grasslands, CO.

Trials took place on the Pawnee National Grasslands and Central Plains Experimental Range in Northeastern Colorado. I conducted a total of 93 playback experimental trials on adult owls over the two-month period of June and July 2011. I was able to collect useful data from 58 of those trials, which included 16 different nesting pairs. Approximate locations of those nesting pairs are indicated by stars.

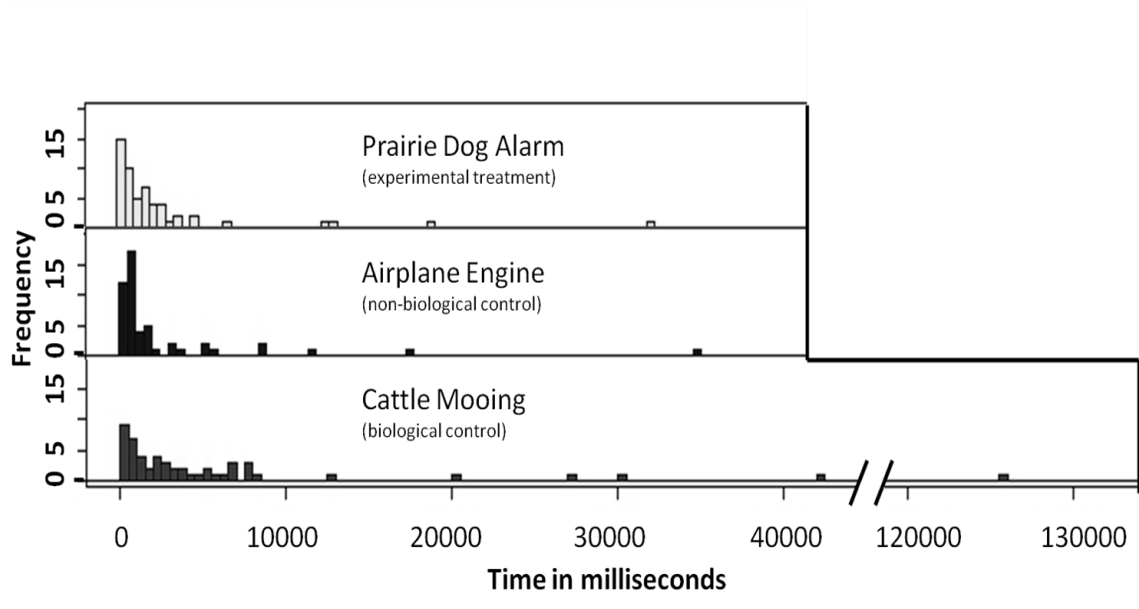


Figure III.2 Latency to Response results.

Latency to response times showed a skewed distribution. Non-parametric analysis of data showed owls had shorter median response times to the prairie dog alarm cue and the non-biological control cue as compared to the biological control sound (Pairwise Wilcoxon test with Bonferroni adjustment: Alarm vs Non-biological cue $P=0.045$, Alarm vs Biological control cue $P=0.028$). There was no significant difference in the median response time to the non-biological control sound cue and the prairie dog alarm sound cue. Responses to the biological sound cue showed more variance in the length of time from sound cue to first alert response.

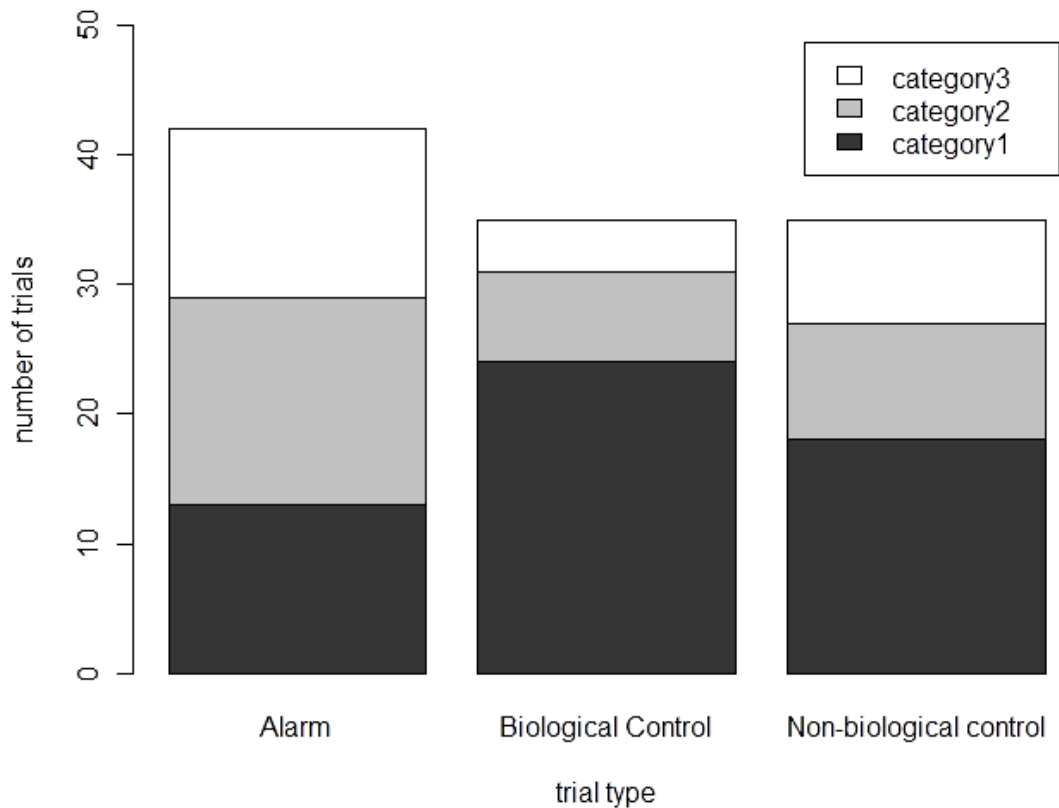


Figure III.3 Intensity of Response Results.

I presented owls with three different sound stimuli: the experimental treatment: (“Alarm”) - a prairie dog barking in response to a snake predator, a biological control: cattle mooing, and a non-biological control: a low-flying airplane engine. All responses are categorized as 1- low (0-2 vigilant behaviors in the first 10 seconds of playback), 2- moderate (3-4 vigilant behaviors in the first 10 seconds of playback), or 3- high rate (5 or more vigilant behaviors in the first 10 seconds of playback). Owls showed more moderate and high rate responses and fewer low rate responses to the prairie dog alarm call than to the biological or non-biological controls. They showed more low-rate responses to the biological control. Fisher’s $P=0.024$.

Table III.1 Ethogram of Scored Burrowing Owl Behaviors.

Ethogram of behaviors scored in J-Watcher 1.0. Each of these behaviors was scored individually, and then classified as “alert” or “relaxed” for data analysis.

ALERT BEHAVIORS	DESCRIPTION	RELAXED BEHAVIORS	DESCRIPTION
vigilance	standing or perching and looking in any direction. Each time bird re-focuses (turns head) is a new vigilance bout.	sleeping	eyes closed or heavily lidded
stretching up tall		preening	actively preening feathers or stretching wings
squatting low		yawning	
locomotion	walking, running, or flying	foraging	looking at the ground or following insects
vocalizing	cooing or alarming		
bobbing	full body or head bob		

Table III.2 Median Times to Alert Response.

I measured the latency from stimulus presentation to alert behavioral response in three categories, Alarm (experimental treatment), Biological Control (cattle mooing), and Non-biological control (airplane engine). The median time to reaction was faster for the Alarm and the Non-biological control than it was for the Biological control. Different superscript letters indicate significant differences in medians.

MEDIAN TIME TO ALERT BEHAVIOR	
SOUND	MEDIAN TIME (MS) (RANGE)
Prairie dog Alarm ^a	1299.5 (216-32912)
Biological Control ^b	2620.0 (250-125824)
Non-biological Control ^a	748.0 (279-35417)
Kruskal-Wallis χ^2	8.697
P-value	0.012

DATA APPENDIX

APPENDIX I: PRAIRIE DOG ALARM CALL ANALYSIS

Results from Balloon Trials

On 13 of the 17 bird balloon presentations, prairie dogs ran to nearby burrows. They proceeded underground into burrows on three of those occasions. On the other 10 occasions, they remained at the lip of a burrow. At least one prairie dog responded vocally to the bird stimulus in 15 of the 17 trials. The number of barks in the subsequent alarm calls ranged from 1-250 during a 3-minute period. Bird balloon alarm calls were significantly different in duration and change in frequency than those emitted in the presence of the snake stimulus, (duration: $F_{3, 95} = 6.5$, $P=0.0005$; delta frequency: $F_{3, 95} = 3.4$, $P=0.02$). Post-hoc comparisons using Tukey's HSD showed bird balloon alarms were on average significantly shorter in duration ($P=0.01$) and higher in delta frequency ($P=0.04$) than snake alarms. Values did not differ significantly from any of the other calls or in any of the other measurement categories. We cannot be sure whether the responses elicited by the bird stimulus were in response to the shape of the balloon, or in response to the loud noise made by the Mylar material in the wind.

Table AI.1 Structural attributes of alarm spectrograms.

Mean \pm standard error for the first alarm bark in response to a predator stimulus. Stimuli that share the same superscript letters are not significantly different ($P > 0.05$). Different superscript letters indicate significant differences in the means ($P < 0.05$).

	mean Δ time (ms)			mean Δ frequency (Hz)		
dog ($n = 15$)	0.074	\pm	0.0035 ^{ab}	6314.1	\pm	221.58 ^{ab}
snake ($n = 33$)	0.076	\pm	0.0029 ^a	7126.5	\pm	188.81 ^b
human ($n = 34$)	0.063	\pm	0.0022 ^b	6267.1	\pm	302.83 ^{ab}
bird ($n = 17$)	0.063	\pm	0.0027 ^b	6008.1	\pm	233.04 ^a
	mean IQR bandwidth (Hz)			mean average power (db)		
dog ($n = 15$)	1986.8	\pm	282.24 ^{ab}	64.93	\pm	2.47 ^{ab}
snake ($n = 33$)	1247.6	\pm	178.99 ^b	59.03	\pm	1.14 ^b
human ($n = 34$)	1889.9	\pm	162.71 ^a	66.66	\pm	1.67 ^a
bird ($n = 17$)	1256.5	\pm	200.05 ^{ab}	60.60	\pm	2.20 ^{ab}
	mean high frequency			mean central frequency		
dog ($n = 15$)	7967.3	\pm	230.57 ^a	4054.0	\pm	156.8 ^a
snake ($n = 33$)	8572.2	\pm	195.82 ^a	3659.3	\pm	89.02 ^a
human ($n = 34$)	7912.0	\pm	298.06 ^a	3668.2	\pm	145.4 ^a
bird ($n = 17$)	7559.13	\pm	246.20 ^a	3992.5	\pm	143.4 ^a
	mean low frequency			mean 1 st quartile frequency		
dog ($n = 15$)	1653.3	\pm	104.7 ^a	3353.4	\pm	177.0 ^a
snake ($n = 33$)	1481.2	\pm	51.35 ^a	3053.8	\pm	131.0 ^a
human ($n = 34$)	1644.9	\pm	79.87 ^a	2898.1	\pm	150.7 ^a
bird ($n = 17$)	1551.1	\pm	35.55 ^a	3414.9	\pm	203.2 ^a
	mean 3 rd quartile frequency					
dog ($n = 15$)	4880.9	\pm	267.2 ^a			
snake ($n = 33$)	4301.4	\pm	144.7 ^a			
human ($n = 34$)	4788.0	\pm	171.2 ^a			
bird ($n = 17$)	4761.4	\pm	218.6 ^a			

APPENDIX II: BURROWING OWL RESPONSE ANALYSIS

Playback Trial Locations

I ran playback trials to 16 different nesting pairs of owls and their chicks on the Pawnee National Grasslands and Central Plains Experimental Range. GPS coordinates and colony names of nests are listed below in alphabetical order:

Central Plains Experimental Range:

N40° 48.001 W104° 42.293
N40° 48.115 W104° 41.426
N40° 48.059 W104° 41.278
N40° 48.074 W104° 46.255
N40° 49.032 W104° 45.564

Pawnee National Grasslands:

Carroll:

N40° 42.850 W104° 36.884

East Stoneham:

N40° 38.732 W103° 34.882
N40° 38.934 W103° 34.914

Halter:

N40° 47.911 W104° 35.031
N40° 48.138 W104° 35.062

Keota:

N40° 38.770 W104° 08.036

Reno:

N40° 44.506 W104° 26.993
N40° 44.461 W104° 26.895

Tappy:

N40° 49.546 W103° 38.664
N40° 49.475 W103° 38.611

West Stoneham:

N40° 38.447 W103° 44.122

Table AII.1 Order of sound cue presentation effect on time to alert behavior.

The order stimuli were presented did not affect response times. Owls showed similar response times to each sound stimulus regardless of where it occurred in the order.

Median time to alert behavior (ms) (<i>range</i>)			
Sound order	Prairie dog Alarm	Biological Control	Non-biological Control
A-B-N	1129.0 (216-32912)	3216 (344-42489)	735 (461-8948)
B-N-A	1597.5 (296-12874)	2369 (250-125824)	876 (279-35417)
N-A-B	1190.5 (221-19432)	1865 (293-30328)	748 (310-11713)
K-W chi squared	1.2569	2.2518	0.0271
p - value	0.5334	0.3244	0.9866

Table AII.2 Pair-wise Wilcoxon test, median time to alert behavior.

Bonferroni-adjusted pairwise comparisons of median times to alert behavior show that the response to the prairie dog alarm was significantly shorter than the response to the biological control, but not the non-biological control.

Sound	Prairie dog Alarm	Biological Control
Biological Control	$P = 0.028$	
Non-biological Control	$P = 1$	$P = 0.045$

Table AII.3 Order of sound cue presentation effect on response intensity.

The order in which stimuli were presented did not affect the intensity of response. Observed values of intensity did not differ from expected intensity values regardless of where the sound cue occurred in the order.

		observed/expected (components)		
stimulus		A-B-N	N-A-B	B-N-A
Alarm: Fisher's Exact test p-value = 0.3066	category 1	10/7.30 (1.00)	3/5.08 (0.85)	7/7.62 (0.05)
	category 2	6/9.85 (1.51)	9/6.85 (0.67)	12/10.28 (0.29)
	category 3	7/5.84 (0.23)	4/4.06 (0.00)	5/6.10 (0.20)
Biological control: Fisher's Exact test p-value = 0.19562	category 1	14/13.61 (0.01)	10/89.72 (0.01)	11/11.67 (0.04)
	category 2	6/5.83 (0.00)	2/4.17 (1.13)	7/5.00 (0.80)
	category 3	1/1.56 (0.20)	3/1.11 (3.21)	0/1.33 (1.33)
Non-biological Control: Fisher's Exact test p-value = 0.3287	category 1	9/9.3 (0.01)	11/7.85 (1.26)	6/8.83 (0.91)
	category 2	7/6.81 (0.01)	3/5.74 (1.30)	9/6.45 (1.01)
	category 3	3/2.87 (0.01)	2/2.42 (0.07)	3/2.71 (0.03)

Table AII.4 Chi-squared comparison of response strength by stimulus.

Owls showed fewer mild responses and more moderate and strong responses than expected in response to the prairie dog alarm call. The showed more mild responses than expected in response to the biological control sound (mooring cattle). Responses were as expected for the non-biological control sound (airplane engine). We ran a Fisher's Exact test because there were fewer than 5 responses in the non-biological control category 3.

Category	observed/expected (components)		
	Alarm	Biological Control	Non-biological Control
1- minimal	13/20 (2.82)	24/17 (2.70)	18/17.19 (0.04)
2- moderate	16/12 (1.33)	7/10 (1.8)	9/10 (0.10)
3- strong	13/9 (1.40)	4/7.8 (1.86)	8/7.8 (0.00)

Fisher's Exact test p-value = **0.02449**

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